

Post-settlement survival of abalone (*Haliotis iris*, *H. australis*) in turbulent flows.

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Abstract

An experimental flow tank which reproduces an oscillating flow typical of shallow coastal waters (ca. 2 m.sec⁻¹) was used to experimentally examine the influence of water flow on the post-settlement survival of abalone (*Haliotis iris* and *H. australis*). Experimental inocula of hatchery-reared larvae settled on substrata of contrasting crustose coralline morphology (encrusting vs warty) were monitored during 24 h exposure trials to calm and turbulent flow regimes. Results indicated greater survival of *H. iris* on encrusting coralline surfaces (*Spongites yendoi*) than on warty surfaces (*Mesophyllum printzianum*): a result attributable to differential predation by infaunal polychaete worms. Survival of *H. australis* on both surfaces was much lower than for *H. iris* suggesting interspecific differences in the interaction between surface morphology and turbulence. The results suggest that both *H. iris* and *H. australis* are well adapted to torrential flows in nearshore habitats, but there is an interaction between the physical and biological aspects of the habitat to which these abalone recruit.

Keywords: *Haliotis iris*, *H. australis*, water flow, post-settlement survival, crustose coralline algae

Introduction

Crustose coralline algae are well known for their roles both in the induction of settlement and metamorphosis in abalone (*Haliotis* spp.) and other invertebrate larvae (Morse *et al.* 1979, Morse and Morse 1984, Johnson *et al.* 1991), and in the provision of suitable habitat for post-settlement growth and survival of abalone (Shepherd and Turner 1985, McShane 1995). Subsequent survival and growth on coralline substrata has been variously attributed to the availability of food, such as that provided in surface biofilms and later by the coralline crust itself (Garland *et al.* 1985, Johnson and Sutton 1994).

From the results of experimental studies, we proposed that the survival of post-settlement abalone (*Haliotis iris* Martyn) was influenced by water movement in the near-shore habitat (McShane and Naylor 1995). Furthermore, we suggested that the effects of water movement would be modified by the topographic complexity of coralline substrata. The topographically complex coralline substrata, more likely to afford protection from wave-driven shear forces, are more prevalent in sheltered habitats such as the understories of kelp forests or on reefs in deep water (McShane 1996). Conversely, encrusting corallines, which we expect to give poor protection to post-settlement individuals from water movement, are prevalent in open shallow reef habitat (McShane 1996).

Here, we show how a simple, inexpensive flow tank can be constructed to realistically simulate water flows representative of near-shore subtidal reef habitats. We use the flow tank to experimentally test the hypothesis that the effect of water movement on the post-settlement survival of *H. iris* and *Haliotis australis* Gmelin depends on the topography of the coralline substrata to which they recruit.

Materials and methods

Experimental flow tanks

Water movement was created within two flow tanks (Fig. 1). The moulded fibreglass tanks were modified by adding a central oval partition to allow directional water flow. The slow flow treatment was created by introducing a laminar flow into each end of the tank at low velocity. The high flow treatment was created by injecting two jets of high velocity water at each end of the tank, and supplementing this by adding the contents of a 20-l bucket of water to each end every 10 seconds. The buckets were suspended on wooden frames on an off center axis 1 m above the flow tank, and had a 0.5 kg weight secured to their outside bottom edge (Fig. 1). The two buckets were constantly filled with fresh seawater and once three quarters full, tipped and discharged. They then swung back

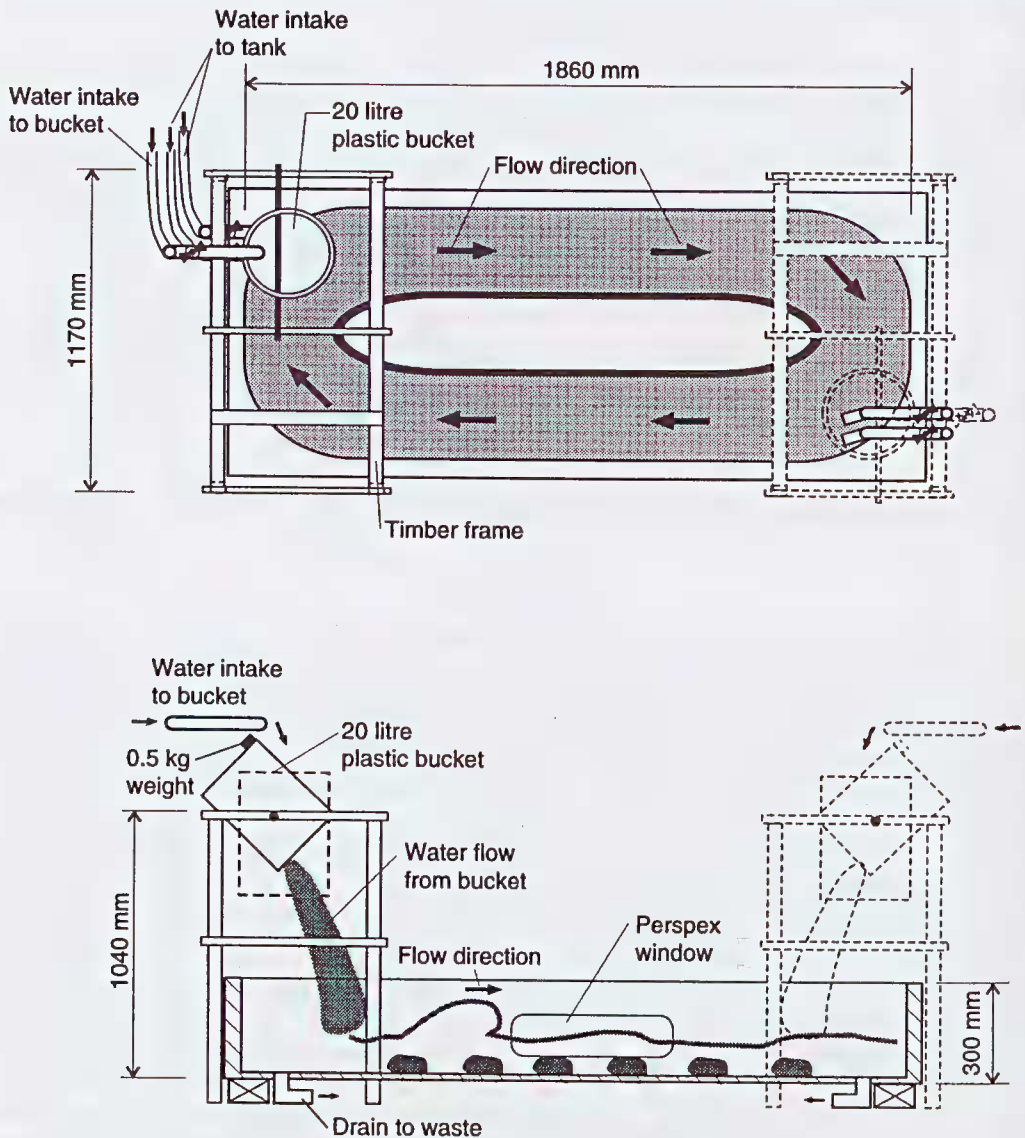


Figure 1. Schematic diagram of the flow tank used in post-settlement survival experiments.

to their original vertical position and began to fill. This simulated the oscillating flow typical of nearshore shallow habitats.

Water flow was measured directly by timing the passage of fluorescent dye over 1 metre. Five replicate measurements were made for each flow regime.

Experimental design

Boulders of similar shape and size (about 200mm in diameter) were obtained from Reef Bay, Wellington, New Zealand. This generally sheltered location provides small boulder/cobble habitat on a gently sloping reef to about 8 m depth (McShane and Naylor 1995). Boulders were chosen the upper surfaces of which were coated with encrusting coralline (*Spongites yendoii*) and warty coralline (*Mesophyllum printzianum*). These coralline surfaces provided contrasting morphology (encrusting vs warty) following the terminology described by (Woelkerling *et al.* 1993).

Larvae were hatchery-reared according to the methods described in Tong and Moss (1992) and Moss and Tong (1992). Inoculation occurred 9 days after fertilisation at which time the larvae had developed 8 rows of chitonised teeth. Post-settlement survival of *H. iris* is greatly increased in larvae with 8 or more rows of teeth (Moss and Tong 1992). Before inoculation, boulders were placed in individual 4-l containers each provided with a jet of running seawater. Separate containers were used to minimise the effects of physical gradients which commonly occur across larger aquaria and which may have resulted in variable larval settlement between boulders. Immediately before inoculation, and for 24 h after, the water supply to the containers was stopped to prevent the loss of larvae by overflow. Approximately 2000 larvae were added to each container.

The experiment was designed to conform to a two factor (morphology, water movement) split-plot analysis of variance (Sokal and Rohlf 1981). There were two levels each of morphology (encrusting and warty) for each tank (calm and turbulent). There were 5 replicates per treatment. All factors were considered fixed and variances were tested for homogeneity with Cochran's test (Underwood 1981). Each species was tested separately.

Experimental substrata were placed at random in two identical flow tanks; one subject to the oscillating turbulent flow (ca. 2 m.sec⁻¹), and the other subject to the calm uni-directional flow (ca. 0.1 m.sec⁻¹). Boulders with either encrusting or warty substrata were placed at random approximately 10 cm apart in the center of the flow line of each tank. Recruits were removed after 24 h from the experimental substrata by soaking in 5% buffered formalin before being counted and measured (to the nearest mm) under a dissecting microscope.

Results

Mean flow rates (s.e.) in the experimental tanks were measured to be 0.10 (0.01) m.sec⁻¹ for the calm flow regime, and 1.83 (0.10) m.sec⁻¹ for the turbulent flow regime. A mean residual flow of 0.53 (0.02) m.sec⁻¹ was maintained in the turbulent flow tank between discharges.

After 24 hours the survival of *H. iris* was greater on encrusting coralline algae than on warty surfaces (Table 1), but there was no significant variation attributable to water flow (Table 2). In general, post-settlement survival of *H. australis* was much less than *H. iris* (Table 1). Although survival of *H. australis* was apparently greater on warty coralline growth forms, these differences were non-significant (Table 2).

Table 1. Survival (numbers of individuals) of *Haliotis iris* and *H. australis* on encrusting and warty coralline surfaces under contrasting flow regimes. Data are means (s.e.).

	<i>Haliotis iris</i>		<i>Haliotis australis</i>	
	Encrusting	Warty	Encrusting	Warty
Calm	185 (48)	120 (45)	5 (3)	17 (7)
Turbulent	224 (50)	62 (23)	3 (1)	6 (4)

Table 2. Effects of turbulence and coralline morphology on the survival of post-settlement abalone *Haliotis iris* and *H. australis*. Split-plot ANOVAs are shown for the dependent variable (numbers surviving after 24 h).

<i>Haliotis iris</i> after 24 h. split-plot ANOVA n = 5; Cochrans untransformed data n.s. (0.389)					
Source	SS	df	MS	F	P
Morphology	75351.7	4	18837.9	6.13	< 0.01
Turbulence	135.2	1	135.2	0.02	n.s.
M x T	14191.3	4	3547.8	1.16	n.s.
<i>Haliotis australis</i> after 24 h. split-plot ANOVA n = 5; Cochrans untransformed data n.s. (0.693)					
Source	SS	df	MS	F	P
Morphology	326.7	4	81.7	1.04	n.s.
Turbulence	186.1	1	186.1	2.05	n.s.
M x T	501.7	4	125.4	1.6	n.s.

Discussion

We attempted to experimentally mimic the water flows typical of the nearshore subtidal habitat of abalone (*Haliotis iris* and *H. australis*). The oscillating horizontal flows of about 2 m.sec⁻¹ reproduced in our flow tank were approximately twice the maxima created by a 1 m unbreaking wave in 2 m of water (from the simplified equations for oscillating wave-induced flows in shallow water; U.S. Army Corps of Engineers 1984) and may be considered torrential (Vogel 1994). However, the water flows in the flow tank may be considerably modified by the experimental substrata just as nearshore water movement is modified by the topography of subtidal reef habitats. Cogent descriptions of the nature of drag and lift forces associated with various substrata are given by Denny (1988) and Vogel (1994). Texts such as these show that the quantification of such forces at the boundary layers of heterogeneous substrata is not simple. For example, the rough texture of the warty *Mesophyllum* substratum may induce a transition from a high drag boundary layer state to a low drag turbulent boundary layer state in the high flow environment (Denny 1988). However, Denny (1989) suggested that such mechanisms to reduce drag may not be available to nearshore benthic organisms. Attempts at visualising flow patterns associated with the two types of experimental substrata with dye streams were not successful as the considerable turbulence masked any obvious differences.

The water turbulence created in our experiment was insufficient to cause significant variation in the post-settlement survival of abalone. However, breaking waves (> 1.5 m in 2 m of water) would create horizontal flows much greater than the 2 m.sec⁻¹ reproduced in our flow tank. It is possible that infrequent exposure to strong flows caused by breaking waves in nearshore habitat could cause dislodgement of recruits from hard substrata (cf. Denny 1988). The adhesion of recruits in the torrential flows examined in our study may be facilitated by strong pedal adhesion facilitated by secreted mucus such as that shown for limpets by Denny (1989).

Clearly, in living in subtidal habitats of extreme exposure, *H. iris* and *H. australis* are well adapted to strong water flows. Experimental trials revealed that post-settlement individuals were much more resistant to removal by suction samplers (McShane and Smith 1988) than similar-sized *H. rubra*. Post-settlement individuals of *H. rubra* which recruit to encrusting coralline surfaces of the understory of macroalgal forests (McShane *et al.* 1988) were all removed by suction whereas only 59% (s.e. 10% for 5 trials) of *H. iris* recruits were removed (McShane and Naylor unpubl. data). Although further studies are necessary, these preliminary results suggest an interspecific difference in pedal adhesion and resistance to lift forces for post-settlement abalone. Suggestions by Shepherd and Daume (1996) that warty coralline algae afforded a poor surface for pedal adhesion by post-settlement abalone were not supported from the results of our study.

The post-settlement survival of *H. iris* was much greater than that of *H. australis*. The contrary result of greater survival of recruits on encrusting than on warty substratum for *H. iris* can be explained by differential predation by infaunal polychaetes (Naylor and McShane 1997). However, as both species were equally vulnerable to predation, other factors were responsible for the interspecific difference in survival. We had previously observed recruits of *H. australis* re-entering the water column up to several days after settlement. In contrast, individuals of *H. iris* adopt a benthic existence after settlement and were never observed re-entering the water column. Thus, *H. australis* may be expected to be more vulnerable to turbulence than *H. iris*. Although the results suggested greater survival on the warty substratum than on the encrusting coralline substratum, the generally low survival rates masked any difference. Our results and observations suggest great differences in the early life histories of these congeneric abalone.

Physical protection from lift and drag forces induced by strong water flows in nearshore habitats may yet prove to be important to survival of post settlement abalone. However, further studies are required to assess the complex physical and biological interactions taking place within the microenvironment associated with the surface of crustose coralline algae.

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